

Preferences of the Fire Ants *Solenopsis invicta* and *S. geminata* (Hymenoptera: Formicidae) for Amino Acid and Sugar Components of Extrafloral Nectars

JANET LANZA,¹ EDWARD L. VARGO, SANDEEP PULIM,² AND YU ZONG CHANG³

Department of Zoology and Brackenridge Field Laboratory, University of Texas,
Austin, TX 78712

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ABSTRACT Extrafloral nectar, a solution of both sugars and amino acids that is produced by plants on stems and leaves, attracts ants that often protect the plants from potential herbivores. To understand better the ecological significance of variability among plants in nectar chemistry, the effectiveness of ant attraction by different extrafloral nectars was compared for nectar mimics that varied in either amino acid or sugar content. Workers of the fire ants *Solenopsis invicta* Buren and *S. geminata* (F.) were fed on artificial nectaries containing mimics of pre- and postdefoliation nectars of *Impatiens sultani*, which differed in amino acid content. Workers of the two fire ant species also fed from artificial nectaries containing mimics of *Passiflora ambigua*, *P. talamancensis*, and *P. quadrangularis*, which varied in sugar composition. *S. geminata* workers preferred the more amino acid-rich postdefoliation mimic over the predefoliation mimic. *S. invicta* did not discriminate between the two nectars, demonstrating that richer amino acid solutions are not more attractive to all ants. In the sugar experiments, both species of ants preferred the nectar of *P. ambigua* over those of the other two *Passiflora* species. The nectar of *P. ambigua* had the lowest total sugar concentration and the lowest calorie content, indicating that ants do not necessarily maximize sugar energy intake as they forage. The behavior of *S. geminata* and *S. invicta* shows that both amino acid and sugar content can affect ant recruitment to plants and that differences in levels of recruitment cannot be predicted accurately based on simple assumptions of nutrient maximization or energy content.

KEY WORDS *Solenopsis* spp., nectars, amino acids

EXTRAFLOREAL NECTAR, a plant adaptation that often serves to reduce herbivory by attracting ant protectors to the plants (Bentley 1977, Elias 1983, Beattie 1985), represents an important component in the diet of many ants (Stradling 1987). As Carroll & Janzen (1973) write, "This food source is extremely generalized and extrafloral nectar is eaten by practically any ant that encounters it." When artificial nectars are placed in the field, ants rapidly recruit to them (Lanza & Krauss 1984, Lanza 1988). In particular, fire ants (*Solenopsis* Westwood) consume large amounts of plant liquids. Both *Solenopsis geminata* (F.) and *S. invicta* Buren collect nectar in nature (Agnew et al. 1982, Lanza 1988, Tennant & Porter 1991) and sugar solutions in the laboratory (Ricks & Vinson 1970; Taylor 1977; Petralia & Vinson 1978; Howard & Tschinkel 1981a,b; Sorensen & Vinson 1981). Porter (1989) showed that sugar

solutions are important for colony growth of *S. invicta*.

Plants vary in the chemical composition of the nectars they produce. Chemically, nectars are relatively complex mixtures with sugars and amino acids representing the most concentrated components, although small amounts of lipids, vitamins, and other compounds may also occur (Baker & Baker 1973, 1975, 1983, 1986). The amino acid content of nectars varies among species and even among members of a single genus. For example, the extrafloral nectar of *Acacia cornigera* contains only five amino acids, all at low concentrations, whereas *Cleome* sp. contains 22 amino acids at relatively high concentrations (Baker et al. 1978). Within a genus of tropical vines (*Passiflora*), the concentration of amino acids can vary from at least 125.2 $\mu\text{M}/\text{ml}$ (*P. caerulea*) to 1,347.3 $\mu\text{M}/\text{ml}$ (*P. menispermifolia*) (Lanza 1991). In addition, herbivory can cause plants to increase the solute concentration of their extrafloral nectars (Stephenson 1982, Smith et al. 1990).

The ecological significance of this chemical variation among nectars is not well understood.

¹ Current address: Biology Department, University of Arkansas, Little Rock, AR 27704.

² Current address: 2018 West Rundberg 16A, Austin, TX 78758.

³ Current address: 112-30 68 Avenue, Forest Hills, NY 11375.

These observations lead to questions about ant response to nectars, the evolutionary effects of ant response on the plants, and variation in response among ant species. Limited experimental work shows that ants recruit at higher rates to more concentrated sucrose solutions (Taylor 1977) and that amino acids can contribute to ant attraction (Lanza & Krauss 1984; Lanza 1988, 1991). But several questions remain: Do ants always prefer more concentrated sugar solutions? How do they respond to different mixtures of sugars, such as those encountered in different plant nectars? Are more amino acids always attractive to ants?

To understand better the role that amino acids and sugars play in attracting potential ant protectors to plants, we measured the preference of two species of fire ants, *S. invicta* and *S. geminata*, to artificial nectars that mimicked the composition of natural nectars but varied in either amino acid or sugar composition. Fire ants were chosen as the test species because they were readily available and because they consume large amounts of plant-derived liquids in nature (Agnew et al. 1982, Lanza 1988, Tennant & Porter 1991). The plant nectars (mimics of *Impatiens sultani* and three species of *Passiflora*) were chosen because the chemical composition was known, and this knowledge provided testable predictions of ant behavior; i.e., that ants would prefer nectars with higher levels of sugars or amino acids over nectars with lower levels of sugars or amino acids. These ants and plants are also good choices because *S. geminata* co-occurs with the *Passiflora* plants in Central and South America. Although fire ants do not co-occur with natural populations of *I. sultani*, ants appear to be opportunistic nectar feeders, collecting nectar whenever they encounter it (Carroll & Janzen 1973).

In the amino acid experiments, we compared the feeding preferences of imported (*S. invicta*) and native (*S. geminata*) fire ants to nectars that mimicked the extrafloral nectar produced by *I. sultani* before and after simulated herbivory. This plant responds to simulated herbivory by increasing the amino acid concentration of its extrafloral nectar, suggesting that the amino acids may be important in attracting greater numbers of ant protectors when plants are attacked by herbivores (Smith et al. 1990). Therefore, we predicted that both species of ants would preferentially consume the postdefoliation mimic because it contained higher levels of amino acids.

In the sugar experiments, we compared the feeding preferences of imported (*S. invicta*) and native (*S. geminata*) fire ants to nectars that mimicked the extrafloral nectars of three species of *Passiflora*. One nectar had relatively equal concentrations of three sugars and the lowest total energy content (*P. ambigua*), one nectar had a high concentration of sucrose and a high total energy content (*P. talamancensis*), and the third

nectar had a high concentration of both glucose and fructose and a high energy content (*P. quadrangularis*). We predicted that both species of ants would preferentially consume the nectar with the highest concentration of sugars.

Materials and Methods

Twenty colonies of *S. invicta* and 19 of *S. geminata* were used in these experiments; all were collected near Austin, TX, and all colonies of both species had multiple egg-laying queens. Colonies varied in size, both between and within species. The ants were maintained in plastic containers (31 by 16.5 by 9 cm) whose inner sides were coated with fluon to prevent escape. Each nest box contained a water-filled test tube plugged with cotton and a petri dish (10 cm) for a nesting chamber (after Banks et al. 1981). Colonies were fed crickets (*Achaeta*) and a sucrose solution, because this diet allows continued growth for at least several months (Porter 1989).

Feeding chambers consisted of fluon-coated plastic boxes (as above) connected to the nest boxes by 1.5-m aluminum runways (after Lanza 1991). These runways were set up daily before each experiment and allowed simulation of the foraging behavior ant colonies would show in nature. Test solutions were placed in the feeding boxes in artificial nectaries constructed from microcentrifuge tubes (after Lanza 1988). Each microcentrifuge tube was closed and contained a nectar. A thread, suspended through the closed top of the microcentrifuge tube and dropping to the nectar inside, acted as a wick and continuously brought small amounts of nectar to the top of the microcentrifuge tube where ants could feed. The nectaries were wired to 3-mm dowels 10 cm above the feeding chamber floor. The dowels were mounted in a row parallel to the edge of the container directly in front of the aluminum runway and were attached with clay to an index card. New index cards were used daily. Dowels and nectaries were cleaned thoroughly with water after each use and air-dried for at least 15 h, thus allowing dispersal of any trail pheromones.

Two experimental nectars were always presented simultaneously. The positions of the test nectars were reversed (left to right) between sequential days of the experiments. The paired design allowed sensitive statistical analyses on nectar preference based on responses of single colonies to two different nectars and reducing the statistical effect of variability among colonies. Data were compared with paired *t* tests (Lanza 1991).

Amino Acid Experiment. Two experimental nectars were used (Table 1), one mimicking the extrafloral nectar produced by *I. sultani* plants before being subjected to simulated herbivory and the other mimicking the extrafloral nectar

Table 1. Nectar composition in amino acid experiments

Amino acid	Concn, mM	
	Predefoliation mimic	Postdefoliation mimic
ala	0.036	0.021
arg	0.151	0.500
asn	0.046	0.196
asp	0.014	0.121
cys	—	0.011
glu	0.021	0.280
gln	0.353	2.123
gly	0.015	0.051
his	0.011	0.051
iso	0.013	0.464
leu	0.008	0.365
lys	0.028	0.039
met	0.005	0.214
phe	0.015	0.494
pro	0.049	0.029
ser	0.041	0.373
thr	0.014	0.581
trp	0.016	0.023
tyr	0.048	1.871
val	0.021	1.145

Nectars in the amino acid experiments contained 0.22 M fructose, 0.21 M glucose, and 1.22 M sucrose.

ALA, Alanine; ARG, Arginine; ASN, Asparagine; CYS, Cysteine; GLU, Glutamic acid; GLN, Glutamine; GLY, Glycine; HIS, Histidine; ISO, Isoleucine; LEU, Leucine; LYS, Lysine; MET, Methionine; PHE, Phenylalanine; PRO, Proline; SER, Serine; THR, Threonine; TRP, Tryptophan; TYR, Tyrosine; VAL, Valine.

produced after the plants were subjected to simulated herbivory (Smith et al. 1990). These nectars differed in that nectar produced after simulated herbivory contains higher concentrations of amino acids than that produced when plants are not subject to herbivory. The nectars analyzed by Smith et al. (1990) were extremely viscous, sometimes crystallized, at least partially because of evaporation; therefore, in making the nectars for these experiments, we used solutions one-eighth as concentrated as those measured by Smith et al. (1990), a procedure that resulted in nectars that were dilute enough to dissolve and for ants to consume. Furthermore, this procedure resulted in sugar and amino acid concentrations that were comparable with those in other extrafloral nectars.

In this experiment, ant response to test solutions was measured as the number of ants seen visiting a nectary. The number of ants on nectaries stabilized within 1 h after the runways to the feeding chambers were set up. Therefore after 1 h of access to the nectaries, the number of ants at each nectary in each feeding chamber was counted at 15-min intervals for 3 h and summed over all observations for a given day. These sums provided one pair of data points from each colony for each day of the experiment.

Sugar Experiments. Extrafloral nectars of three species of *Passiflora* were analyzed by HPLC (G. C. Smith & J. L., unpublished data). Based on

Table 2. Nectar composition in sugar experiments

Sugar	Concn, M		
	<i>P. ambigua</i> mimic	<i>P. quadrangularis</i> mimic	<i>P. menispermifolia</i> mimic
Fructose	0.679	1.724	0.515
Glucose	0.629	2.453	0.517
Sucrose	0.487	0.099	1.547
Total M sugars	1.795	4.276	2.579
kJ/liter	6,578	12,574	11,922

these analyses, three sugar-only experimental nectars were made, mimicking the extrafloral nectar of *Passiflora ambigua*, *P. quadrangularis*, and *P. talamancensis* (Table 2). Although these species produce nectar containing amino acids, the amino acids were omitted from the nectar mimics so that only one variable (sugar composition) was manipulated in the experiment. Ant response to the nectar of *P. ambigua* was compared with the nectars of each of the other two species.

Ant response was measured in two ways. First, numbers of ants at the test nectaries were counted as in the amino acid experiments. Second, nectaries were weighed before and after ant feeding, providing a measurement of consumption. Evaporation was assumed to affect both nectars equally, as shown by Rathman et al. (1990).

Results

Amino Acid Experiments. *Solenopsis geminata* preferentially visited nectaries containing postdefoliation mimics of *I. sultani* extrafloral nectars over those containing predefoliation mimics (Table 3), with 11% more workers visiting the nectar richer in amino acids. *S. invicta* did not distinguish between pre- and postdefoliation nectars (Table 3). A two-way repeated-measures analysis of variance (ANOVA) on total numbers of ants observed on both experimental nectaries on each day (after Lanza 1991) showed

Table 3. Number of *S. geminata* and *S. invicta* per colony per day counted on the experimental nectaries containing mimics of pre- and postdefoliation nectar of *I. sultani* (amino acid experiment)

Species	n	No. ant/nectary/d ^a		t ^b	P
		Predefoliation nectar	Postdefoliation nectar		
<i>S. invicta</i>	83	303 ± 109.6	309 ± 115.9	0.561	0.2883
<i>S. geminata</i>	47	317 ± 60.8	351 ± 71.3	3.367	0.0007

^a Values are means ± SD.

^b The data were tested statistically with one-tailed paired *t* tests using the prediction (Lanza 1991) that more ants would visit the postdefoliation nectar because it contains higher concentrations of amino acids.

Table 4. Results of two-factor repeated measures ANOVAs conducted on the total numbers of ants (*S. invicta* and *S. geminata*) observed visiting the experimental nectaries on each day and the total amount of nectar consumed per day

Parameter	No. ants	Nectar consumed
Amino acid experiment: pre- versus postdefoliation nectars of <i>I. sultani</i>		
<i>S. invicta</i>		
Colony	$P < 0.001$	
Day	$P < 0.001$	
<i>S. geminata</i>		
Colony	$P < 0.01$	
Day	$P < 0.001$	
Sugar experiment: <i>P. ambigua</i> versus <i>P. quadrangularis</i>		
<i>S. invicta</i>		
Colony	$P < 0.001$	NSD
Day	NSD	$P < 0.001$
<i>S. geminata</i>		
Colony	$P < 0.001$	$P < 0.001$
Day	$P < 0.05$	NSD
Sugar experiment: <i>P. ambigua</i> versus <i>P. talamancensis</i>		
<i>S. invicta</i>		
Colony	$P < 0.01$	NSD
Day	NSD	NSD
<i>S. geminata</i>		
Colony	$P < 0.01$	$P < 0.001$
Day	NSD	NSD

Colony was the factor tested, with day used for the repeated measure; the interaction term (AB) was used as the error term (Zar 1984). NSD, no significant difference ($P > 0.05$).

that variation among colonies and among days was significant (Table 4).

Sugar Experiments. When numbers of ants counted on the experimental nectaries were the measured variable, *S. geminata* demonstrated a preference for the sugars of extrafloral nectar of *Passiflora ambigua* over those of the extrafloral nectar of *P. quadrangularis* (Table 5); *S. geminata* did not discriminate between the sugars of *P. ambigua* and *P. talamancensis* nectars (Table

Table 6. Correlation coefficients between number of ants observed on experimental nectaries and amount of nectar consumed

Ant species	n	<i>Passiflora</i> species	
		<i>P. ambigua</i>	<i>P. quadrangularis</i>
<i>S. geminata</i>	48	0.628***	0.518***
<i>S. invicta</i>	43	0.748***	0.355*
		<i>P. ambigua</i>	<i>P. talamancensis</i>
<i>S. geminata</i>	18	0.653*	0.522*
<i>S. invicta</i>	16	0.710***	0.502*

*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

5). With this measure, *S. invicta* did not discriminate between the nectars presented (Table 5). A two-way repeated-measures ANOVA on total number of ants observed on both experimental nectaries on each day showed that variation among colonies was significant (Table 4); days, however, had a significant effect in only one case.

In contrast, when the amount of nectar consumed was the measured variable, both species discriminated between the nectars presented (Table 5). Both species preferred sugars of *P. ambigua* over those of *P. quadrangularis* and over those of *P. talamancensis*. The number of ants observed was correlated with the amount of nectar consumed (Table 6). Fewer significant effects were discovered in a two-way repeated-measures ANOVA on total nectar consumed per day by each colony (Table 4) than when a similar analysis was conducted on total number of ants observed (see above).

Discussion

In contrast to previous experiments (Lanza 1991), increased amino acid presence in nectars

Table 5. Number of *S. geminata* and *S. invicta* per colony per day counted on the experimental nectaries containing mimics of the sugar components of *Passiflora* extrafloral nectars, and mass of nectar consumed by *S. geminata* and *S. invicta* per colony per day

Species	n	<i>Passiflora</i> species ^a		t	p ^b
		No. ants			
		<i>P. ambigua</i>	<i>P. quadrangularis</i>		
<i>S. invicta</i>	50	143.5 ± 43.3	129.5 ± 47.1	1.68	0.04
<i>S. geminata</i>	45	126.9 ± 66.3	114.7 ± 56.3	2.14	NSD
		<i>P. ambigua</i>	<i>P. talamancensis</i>		
<i>S. invicta</i>	20	117.3 ± 54.4	107.0 ± 57.1	0.95	NSD
<i>S. geminata</i>	18	155.8 ± 55.2	141.8 ± 57.1	1.16	NSD
		Nectar consumption, g			
		<i>P. ambigua</i>	<i>P. quadrangularis</i>		
<i>S. invicta</i>	50	0.052 ± 0.037	0.029 ± 0.028	4.60	0.001
<i>S. geminata</i>	18	0.043 ± 0.038	0.018 ± 0.011	5.25	0.001
		<i>P. ambigua</i>	<i>P. talamancensis</i>		
<i>S. invicta</i>	20	0.024 ± 0.016	0.011 ± 0.009	5.71	0.0001
<i>S. geminata</i>	18	0.046 ± 0.041	0.017 ± 0.011	3.15	0.006

^a Values are means ± SD.

^b NSD, no significant difference ($P > 0.05$).

contributed to attraction of only one species of *Solenopsis*. *S. geminata* discriminated between different amino acid-containing nectars, whereas *S. invicta* did not. *S. geminata* preferred the nectars (postdefoliation) with higher levels of amino acids over nectars (predefoliation) with lower levels of amino acids. Our results are partially consistent with previous experiments—both species have previously demonstrated preference for nectars containing higher levels of amino acids (Lanza 1991). However, apparently not all high amino acid nectars are attractive; in this set of experiments, *S. invicta* did not discriminate between the postdefoliation (high amino acid levels) and predefoliation (lower amino acid levels) nectars. Future tests of ant preference should explore further how amino acid concentrations alter ant recruitment.

The results of these experiments leave open the question of why *I. sultani* produces nectars richer in amino acids after suffering simulated herbivory. Smith et al. (1990) discussed two possibilities: (1) that the increase in amino acid concentration might be adaptive, serving to attract more ant protectors to attack the herbivores; and (2) that the increase might be a consequence of physiological changes brought on simply by leaf loss. Our results show that the increase in amino acid concentrations may attract more ant protectors (e.g., *S. geminata*) but that this response is not necessarily shared even by a congener (e.g., *S. invicta*). With variable ant response, selection pressures on plants may not be consistent enough to favor increased nectar concentrations and may indicate that such an increase is a physiological accident that has not resulted from the action of natural selection.

In contrast to expectations from optimal foraging theory, in the sugar experiments, both ant species fed preferentially from the nectar that was lowest in sugar concentration and energy content. Both species of *Solenopsis* preferentially consumed nectar of *P. ambigua* compared with the other two *Passiflora* species; this preferred nectar was intermediate to the other two nectars in fructose, glucose, and sucrose concentration. *P. ambigua* nectar had a lower total molar concentration of sugars (1.795 M) and a lower energy content (6,578 kJ/liter) than either *P. quadrangularis* (4.276 M and 12,574 kJ/liter) or *P. menispermifolia* (2.579 M and 11,922 kJ/liter). Using two concentrations of sucrose (0.5 and 1.5 M), Taylor (1977) suggested that *S. geminata* and *Pogonomyrmex occidentalis* (Cresson) forage in ways that maximize their energy gain; clearly, this generalization is not upheld when mixtures of sugars are involved, the usual situation in nature.

Although several variables (viscosity, individual sugar concentrations, total sugar concentration, and sugar balance) represent possible explanations, sugar balance seems the most likely

explanation of the ants' surprising sugar preferences. Sugar solutions become more viscous as concentrations increase. However, the nectars of *P. talamancensis* and *P. quadrangularis* did not appear obviously more viscous than that of *P. ambigua*. Although some preference based on the lower viscosity of the more dilute *P. ambigua* nectar cannot be completely ruled out, it should be noted that these ants will feed from liquids as viscous as honey (Sorensen & Vinson 1981; Sorensen et al. 1981, 1985a, b). The second possibility is that *Solenopsis* prefer nectars with high levels of one particular sugar. However, *P. quadrangularis* is richer than *P. ambigua* in fructose (1.724 M versus 0.679 M) and glucose (2.453 M versus 0.629 M) and *P. menispermifolia* is richer in sucrose (1.547 M versus 0.487 M). The third possible explanation is that the preference for *P. ambigua* results simply from its lower total concentration (1.795 M versus 2.579 M and 4.276 M). However, examination of the individual sugar concentrations does not support this explanation. In our experiments, the concentration of sucrose in the nectar of *P. ambigua* is close (0.487 M) to that of Taylor's low sucrose concentration (0.5 M), whereas that of *P. menispermifolia* (1.547 M) is close to Taylor's higher, preferred concentration (1.5 M). For this explanation to be correct, the cause of the preference for *P. ambigua* must lie in the concentrations of fructose or glucose or both. These concentrations are slightly higher in the preferred *P. ambigua* (0.679 and 0.629 M, respectively) than in *P. menispermifolia* (0.515 and 0.517 M, respectively) but lower than in *P. quadrangularis* (1.724 and 2.453 M, respectively). Finally, the preference may result from a more even balance of sugars in the *P. ambigua* nectar. This nectar contains the most uniform individual sugar concentrations, suggesting that a relatively even balance of sugar concentrations is attractive to *Solenopsis*.

The difficulty in understanding the ant preferences for sugar mixtures is not surprising. Predictions of animal responses to mixtures are difficult to make because animals do not always respond to mixtures in the way their responses to single compounds would predict. For example, the minimum detection level of flies for fructose and sucrose varies depending on whether they are presented singly or together (Dethier 1976). In addition, Lanza & Krauss (1984) discovered preferences by ants for three amino acids when tested singly and no preference for or against a fourth amino acid, but when these four amino acids were combined, the ants avoided the mixture.

Future experiments should test whether it is the absolute concentrations of sugars or the balance of sugars that makes *P. ambigua* attractive. For example, nectars could be made to have the same total moles of sugars of *P. ambigua* while

keeping the relative concentrations identical to those of *P. talamancensis* or *P. quadrangularis*. Additional experiments should test the combined effect of amino acids and sugars; *P. ambigua* produces a nectar richest in amino acids, whereas the nectar of *P. quadrangularis* is lowest and that of *P. talamancensis* is intermediate (J. L. & G. C. Smith, unpublished data).

The two methods of measuring preference that we used in the sugar experiments (mass of nectar consumed and numbers of ants observed) showed that nectar consumption appears to be a better measure of ant response than the number of ants counted on experimental nectaries. Consumption was better able to detect differential responses by ants to sugar solutions: consumption indicated preferences by both species of *Solenopsis* for *P. ambigua* nectar over both other *Passiflora* nectars, whereas ant numbers indicated only one significant preference. In addition, using nectar consumption rather than number of ants counted removed some of the variability in the data that was caused by colony and day. Finally, nectar consumption measures are less demanding of investigators' time than are counts, allowing greater sample size or attention to other behaviors.

In summary, these experiments show that both sugar and amino acid consumption can affect the recruitment of *Solenopsis* to plant nectars but that the ants may not simply maximize energy or nutrient intake. To understand ant feeding in nature, future experiments should test not only the effect of changing sugar or amino acid compositions but also the effect of changing both nectar components simultaneously.

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